r/K Selection Theory Is Bogus

Blithering Genius

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In this essay, I will debunk R/K selection theory.

First, I encourage you to read the Wikipedia article on it, even if you know what it is. The article mentions that the theory is no longer generally accepted as valid in biology. I am not appealing to authority — I will debunk it myself — but I thought I should point that out.

1 The Basis For r/K Selection Theory

The R and K come from the Verhulst model of population dynamics:

$$G = R \times N \times (1 - N/K)$$

G is the growth rate of a population. R is the maximal fertility per individual. N is the size of the population. K is the carrying capacity of the environment.

This equation expresses the intuition that increased population density makes life harder. As N approaches K, G approaches 0. If N exceeds K, then G is negative. When N is much smaller than K, G approaches R.

Other than expressing an obvious intuition that density impedes growth, the equation isn't very useful. There is no way to observe K that is independent of N. The only way to estimate K is to observe N when G is 0. Another problem is that the concept of “the environment” is not well defined outside a laboratory. What is the environment for an oyster? Is it a lagoon, a bay or the entire ocean? There is a more general reason why modeling population dynamics with differential equations is not very useful, which I will discuss at the end of this essay.

The basic idea behind R/K selection theory is that some species are adapted to live close to the carrying capacity (K-selected) and others are adapted to live below the carrying capacity (R-selected). There is a secondary assumption that K-selection would favor greater parental investment. I will explain why both of these ideas are false.

2 R/K Selection Theory Is Poorly Defined

According to R/K selection theory, R-selection causes high fertility and low parental investment, while K-selection causes low fertility and high parental investment. This immediately raises some questions. What is "high" fertility? Is high fertility for an oyster the same as high fertility for a muskrat? If not, why not? What environmental conditions select for one reproductive strategy versus another? How do you know whether a species is R or K selected?

According to Wikipedia, R-selected species exploit less crowded ecological niches. But what does that mean? What is a "less crowded" ecological niche? What makes it "less crowded"? I suppose that it would be something like more available energy for a specific phenotype to use. But of course no ecological niche is uncrowded for long, because every species has the potential for population growth, even if it has relatively low fertility. Every niche becomes filled to capacity eventually.

There might be a meaningful distinction between opportunistic species that are adapted to exploit new niches quickly, and those that are adapted to live in stable environments where there is little available energy to support new individuals. Perhaps that is the idea. Let's assume so. What traits are most useful to an opportunistic organism? What traits are most useful at exploiting an environment with occasional surpluses of energy? Keep in mind that the organism has to find the niche, colonize it, and then escape from it when it closes up.

3 The Reproductive Strategies of Example Organisms

It is true that high fertility could be useful in rapidly colonizing a new niche. For example, aphids use cloning to rapidly colonize plants. They can switch between sexual and asexual reproduction, depending on the situation. Fruit flies are another example. They rapidly colonize ripe fruit before it rots. They have high fertility compared to mammals, but not unusually high for insects. They have very short lives, and that is a key adaptation, because ripe fruit doesn't last long. Another example is the fireweed plant. Fireweed colonizes landscapes that have been recently logged or burned over. Fireweed produces a lot of seeds that have cottony down attached to them, so they float away on the breeze to colonize a new area. Aphids, fruit flies and fireweed all have high fertility, although not exceptionally high compared to other similar organisms. Their main adaptation is rapid growth and/or reaching maturity quickly.

There are many species that have lots of babies, but live in stable environments where there is little room for additional individuals of their kind. Oysters are a good example. Oysters live in sheltered, shallow bays that change very little from year to year. Once the bay is colonized by oysters, they usually maintain a high population thereafter, unless conditions change. Nevertheless, oysters have very high fertility. According to Wikipedia, a female oyster can produce up to 100 million eggs annually. Shouldn't oysters be K-selected? They do take longer to reach sexual maturity than fruit flies, but they have high fertility and invest relatively little per offspring.

There are also opportunistic species that have relatively low fertility and take a long time to reach maturity. Some examples are coyotes, raccoons, elephants and human beings. Human beings are great at finding new niches with available energy and using it to make new humans. What makes these creatures good at being opportunistic? Behavioral plasticity.

Behavioral plasticity means that an organism can change its behavior to adapt to its environment. Those pesky aphids have one type of behavioral plasticity: they can switch between reproducing asexually and reproducing sexually. (I think they can also grow wings or not.) They have two behavior patterns, one that works in a condition of abundance, and one that works when my zucchini plant is almost dead. (The little fuckers! Or non-fuckers, as the case may be.) Big, intelligent organisms, such as human beings and elephants, can change their behavior within their lifetimes in complex ways. They can think. They can learn from each other. Their adaptability makes them good at exploiting new opportunities. It also requires a big brain, a long life, a long childhood and a large parental investment per child.

Hmm...

Another simple and fairly obvious way to exploit sporadic abundance is to move around. Humans do that. So do elephants, coyotes and many other large mammals. They need big strong bodies to move around, and those bodies need lots of energy, so they invest a lot in their offspring. Fruit flies eat ripe fruit, but so do monkeys, elephants and humans. Are humpback whales R-selected because they move around in search of temporarily abundant food sources? Or are they K-selected because they have a few offspring and invest a lot in each one?

4 Every Species Is K-Selected and R-Selected

The fact is that *every* species is opportunistic and *every* species has to survive in environments of scarcity. The two things are not mutually exclusive. They are universal problems for living beings.

In an environment where the population is at the carrying capacity, there are always little niches opening up due to the deaths of individuals. In that shallow bay full of oysters, individual oysters are always dying and opening up little niches for new oysters to exploit. Most baby oysters die young, but a few find an opening in the ecosystem and settle down, grow up, and produce 100 million babies themselves. That is what oysters do. That is how they live. It works. That is all we can say. Oysters are opportunistic and they live at the carrying capacity of their environment.

Fruit flies have to survive scarcity. They can reproduce like crazy when the fruit is ripe, but life becomes hard when the fruit starts to decay. Then they need to escape that local niche and find another. If fruit flies made movies, they would all be romantic comedies set on ripe bananas, or dramas about escaping from rotten bananas. The fruit fly goes through both R-selection and K-selection.

Does it always make sense for fruit fly mamas to have lots of babies? Not necessarily. During the population explosion, high fertility is the best strategy. But when abundance ends, and the die-off begins, lower fertility might be a better strategy. Investing more in a baby might allow it to fly away to find a new home on a ripe banana somewhere else. In fact, a female fruit fly that survives to maturity produces only about 500 eggs, compared to the 100 million of the "K-selected" oyster.

Are human beings K-selected or R-selected? It is a meaningless question, because the premise of the question is flawed. Every species is K-selected and R-selected. There are only different ways of life: different phenotypes. Some work and some don't. Those that work, work in some environments and not in others. A fixed physical environment will develop an ecosystem that contains a mix of different types of organisms, and thus different life strategies. That is all we can really say. The notions of R-selection and K-selection have no predictive or explanatory power. They are meaningless. They add nothing to evolutionary theory except confusion.

Some people think that R/K selection theory explains the differences between human races, or even between the left and right in politics. This is bogus, because R/K selection theory is bogus. There are differences between individuals and races, but they are not explained by R/K selection theory.

5 How To Think About Evolution

The point of this essay was not just to debunk R/K selection theory. There is a more general point about how to think about evolution, and how not to think about evolution.

People often use bogus heuristics to think about evolution, such as R/K selection theory or the "ladder of progress" metaphor. Why is that? I think it is because most people don't understand the theory of evolution. In my experience, even credentialed biologists often have misconceptions about it. They don't really understand it. Although it is very simple, the theory of evolution is counter-intuitive to most people. So, they substitute bogus heuristics for principled reasoning based on the theory.

Evolution is a process that has three component processes:

- Reproduction (to excess).
- Variation in offspring.
- Selection.

Evolution is reproduction with variation and selection, repeated. That's it. Everything you need to know about evolution can be deduced from that definition. However, it is not obvious to most people how to use this theory to generate predictions and explanations. So instead, they often use heuristics that do not follow from the theory.

Evolutionary theory has explanatory and predictive power, but it is limited. It can't tell us exactly why something happened, or exactly what will happen in the future.

6 Selective Equilibria

The most important concept in evolutionary theory is the badly named "evolutionarily stable state" or "ESS". It is really a state that is stable with respect to *selection*, not evolution, so I will use the term "selective equilibrium" instead, and hope that it catches on. A selective equilibrium is a state in which the frequencies of reproductive strategies are balanced. Every reproductive strategy in the population is equally adaptive, given the current frequencies of all the strategies. When a population is not in a selective equilibrium, some strategies are more adaptive than others, and so the frequencies of strategies will change. Selection pushes populations and ecosystems toward selective equilibria.

In the Verhulst model, $N = K$ is a selective equilibrium. In that state, $G = 0$. Selection moves the system toward that state. Excess reproduction would create a positive growth rate, but R is balanced by the density-dependent forces of selection, represented by (1 – N/K). Life is pushed toward the capacity of the environment by selection, for all species.

Evolutionary stability is not permanent. Variation occasionally introduces new strategies. If a new strategy is competitive against existing ones, the system will be unstable for a while, as the new strategy increases in frequency. Physical events, such as volcanic eruptions or climate change, can also push ecosystems out of stable states. And there is not necessarily one selective equilibrium for a given environment and set of strategies. There could be multiple stable states, and getting bumped out of one might cause the system to fall into another one.

So, although evolutionary theory has some explanatory and predictive power, that power is limited. Selection makes evolution somewhat predictable, because it creates stability and order. But variation adds new information, and that new information can be amplified by excess reproduction. Variation and excess reproduction cause unpredictable changes. Evolution produces both order and chaos.

For that reason, evolution doesn't lend itself to precise mathematical formulas, except in a highly controlled environment, such as a Petri dish. And ad hoc qualitative reasoning, such as R/K selection theory, is usually bogus.