PNAS COMMENTARY

Two principles of success

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A new PNAS article by Santos et al. (1) links two great principles of success. First, steady return typically beats variable return (2). Second, competitors acting in a correlated way tend to be more cooperative and successful (3, 4). Each principle applies widely in biology, economics, and other competitive situations. But how they interact is a challenging problem that has received little attention. This new article makes a good first step, leaving open a grand challenge for mathematically skilled workers looking to advance fundamental understanding in biology and economics.

Let's start with the benefits of steady success. When investing $10,000 over 10 y, a steady return of 7% per year yields $417 more than getting 0% and 14% in alternate years. In each case, the average return per year is 7%. However, the variability in the second case discounts yield.

It works the same way in biology (5). Over two generations, a yeast cell that expands its descendant lineage threefold in each generation grows ninefold. Another cell's lineage that expands fourfold one generation and then doubles in the next grows only eightfold. Both get expanded by an average of 3 in each generation. But the latter pays the cost of fluctuating success. We may think of the principle as a tradeoff. It often helps to reduce average success a bit in exchange for steadier return.

That seems simple. But the more realistic analysis for biology is not so easy (6). Natural selection favors types that have the greatest relative success. If we have two competing types in a population with successes described by the random variables X and Y, with frequencies in the population q and $1-q$, then the change in the frequency of the type associated with X is

$$\Delta q = q(F-1), \quad [1]$$

in which that type's relative success is

$$F = \frac{X}{qX + (1-q)Y}. \quad [2]$$

Although it looks simple, it turns out to be difficult to draw general conclusions about the ratio of random variables. If so inclined, one can spend inordinate amounts of time analyzing this equation to study how natural selection plays out in this fundamentally realistic problem of randomness in relative success (7, 8). Similarly, economic or game-like competition for market share or other aspects of relative success poses the same challenge.

The usual trick is to assume that the amount of variation is small. Then one can write a simple approximation for F and draw all sorts of conclusions. Most of the literature in biology and economics does that. However, some of those conclusions do not hold in the common situation of larger fluctuations or in realistic scenarios of how competition is structured. So, for this essential problem, we often lack good basic guidelines. For example, sometimes more variation is favored (9, 10).

This challenge is one part of what Santos et al. (1) go after. The second part concerns another great principle of success, the role of correlation between competitors. Let's introduce this second part, then look at the link made by Santos et al.

Often, an individual's behavior influences its own success and the success of its neighbors. And the neighbor's behavior influences that individual's success. Suppose an individual can reduce its own success in a way that enhances the success of all neighbors. Then a tension arises between the competitive gain of a focal individual and the success of the group (11).

That sort of tension occurs throughout life (12–16). Among simple replicating molecules or among cells competing for an essential nutrient, more competitive individuals gain more of the nutrient and grow faster. However, the extra effort to increase nutrient uptake diverts resources from growth. So, greater competitive ability raises success against neighbors but lowers the overall efficiency of the group.

All group members would do better if they grew more slowly, using the local resources more prudently. Yet natural selection typically favors the rapacious when competing for common resources. Everyone does worse than they might—the tragedy of the commons (11). Microbes typically act this way (17). So do humans (18). It's a universal outcome of intrinsic competitiveness.

Correlated behavior between group members can mitigate this frequent tension between an individual and its neighbors. To see this, assume an individual's success, w, depends on its own behavior, y, and the average behavior of its neighbors, z. Suppose that an increase in y corresponds to an individual reducing its own success and enhancing its neighbors' success, what might be called cooperative or altruistic behavior.

To evaluate how an individual's success changes with its tendency for cooperation, we can look at the slope of w with respect to y (19). When that slope is greater than zero, the forces acting on success favor greater cooperation. To evaluate when the slope of w with respect to y is greater than zero, we use the chain rule of differentiation

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$$\frac{dw}{dy} = \frac{\partial w}{\partial y} + \frac{\partial w}{\partial z}\frac{dz}{dy}$$
$$= -c + br > 0.$$

The symbols in the second line correspond in the same order to the terms in the first line.

Here, c measures the cost to an individual for increasing its cooperation. The minus sign arises because a positive cost decreases success. The b term measures the benefit provided by neighbors. The r term describes the change in neighbors' behavior with respect to the focal individual's behavior, a quantity related to the correlation in behavior between partners.

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In biology, r traditionally describes the genetic association between individuals. The more genetically similar individuals are, the more correlated their behavior tends to be. In addition, the genetic basis provides heritability and thus completes the requirements for natural selection to change characters over time. In different biological scenarios, we get the same expression but with different interpretations for costs, benefits, and correlations (16).

In biology, one traditionally expresses the condition for cooperation to increase as

$$rb - c > 0,$$

and calls that Hamilton's rule (20). However, it is important to recognize the underlying generality of the expression as a description of partial causes (17). All that we did is partition a total change in success into components that isolate instantaneous partial causes within a given context. The reason that the same expression arises in different scenarios is that the basic form of partitioning gives the same structure in different cases. Here, derivatives for small changes simplify the steps but we could do the same using regression coefficients for larger changes (16, 21, 22).

Such partitions can be very useful. But effective use requires paying attention to what they actually express. Instantaneous partial causes isolate forces and help to understand certain outcomes. But such instantaneous measures typically change with context.

Now we can return to combining our two principles, following Santos et al. (1). Starting with the cooperative part, we need to look at $rb - c$ to evaluate how the focal individual's loss in its own success, c, trades off against the neighbor benefit, b, weighted by the association measure, r.

We also need our first principle to adjust cooperative success by its variation. That is a technical challenge that remains unsolved. But Santos et al. make a significant advance. Return to Eq. **1**, an expression for Δq. We can think of q as the frequency of a more cooperative behavior compared to an alternative type in the population that is less cooperative. Then we ask when is $\Delta q > 0$, describing when cooperation increases. However, Δq is stochastic because the environment varies, causing the relative success of more cooperative versus less cooperative behaviors to vary.

A first step would be an expression for when the expected value of the change is greater than zero, $E(\Delta q) > 0$. Santos et al. give that condition as

$$rb - c + \nu\rho\sigma > 0.$$

In any measure of relative success, the denominator is the average absolute level of success, $\bar{w}$, making the component $1/\bar{w}$. Here, ν measures that component's coefficient of variation over environmental states. The term ρ measures the correlation between $1/\bar{w}$ and the net gain to a focal individual for being more cooperative, $rb - c$. Finally, σ measures the SD in the net cooperative benefit, $rb - c$.

The three components of the variability effect, $\nu\rho\sigma$, can be studied empirically (1), providing an opportunity to test the theory. This expression also shows that the variability effect can either favor or disfavor cooperation because the correlation term, ρ, can be positive or negative.

What conditions could lead to the surprising case in which ρ is positive and variability enhances success? Using the notation in Eq. **2**, that typically happens when the success of a type, X, is negatively correlated with average success, $\bar{w} = qX + (1 - q)Y$, which requires

$$q + (1 - q)\rho_{XY} < 0,$$

with ρ_{XY} as the correlation between the two competing types, X and Y.

This condition requires that q be small, which means that the focal type has to be rare, and that ρ_{XY} be negative, which means that the types respond in opposite ways to environmental changes. Thus, in competitive situations for relative success or market share, rare types gain by being different from their dominant competitors. The dominant types gain by allocating some of their resources to copy their opponents and keep ρ_{XY} positive (23).

Overall, much remains to understand this challenging problem. For example, different assumptions about the causes of correlation and the context dependence of the components likely matter. And knowing only the expected direction of change at any moment is not sufficient for a full analysis of a stochastic process. Nonetheless, given the two principles' very broad consequences for understanding patterns of nature and human social conditions, the steps here may stimulate a significant advance.

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