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Quick guides

Trade-offs

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How do organisms evolve as coordinated wholes? As noted by Charles Darwin (1859) in *The Origin of Species*, "The whole organism is so tied together that when slight variations in one part occur, and are accumulated through natural selection, other parts become modified. This is a very important subject, most imperfectly understood." Biologists have made major advances since then, and one of the primary conceptual tools used to understand how traits evolve in a correlated fashion is the idea of trade-offs. Indeed, the concept of trade-offs underpins much of the research in evolutionary organismal biology, physiology, behavioral ecology, and functional morphology, to name just a few fields.

What is a trade-off? In engineering and economics, trade-offs are familiar enough (e.g., money spent on rent is not available to buy food). In biology, a trade-off exists when one trait cannot increase without a decrease in another (or vice versa). Such a situation can be caused by a number of physical and biological mechanisms. One type of mechanism is described by the so-called 'Y-model', which states that for a given amount of resource (e.g., energy, space, time), it is impossible to increase two traits at once. A commonly cited example is a trade-off between the size and number of eggs that, for example, a fish, bird or turtle can produce in a given clutch. Depending on the organism, this trade-off can be caused by a limitation in the amount of energy available, the amount of time available to produce eggs or the amount of space available to hold eggs (e.g., inside the shell of a turtle). Similarly, time spent foraging may be time wasted with respect to finding a mate. Trade-offs also occur when characteristics that enhance one aspect of performance necessarily decrease another type of performance.

What happens when functional demands conflict? Having survived a decade of frigid winters in Wisconsin, I like to use the example of gloves versus mittens. Gloves are good for making snowballs and getting keys out of your pocket, but they do not keep your hands nearly as warm as mittens do. Moreover, you must remove the mittens to get the keys. Returning to biology, limbs can be 'designed' for speed, through lengthening and thinning of bone, but this will often reduce strength and make them more likely to break when in use. Hence, a predator that evolves to be a fast runner may have to trade-off its ability to subdue large or strong prey (e.g., cheetah *versus* lion).

How do I recognize a trade-off? Empirically, trade-offs usually are initially identified by comparing species or individuals within species, and testing for a negative relationship between two (or more) traits. A classic example is the trade-off between speed and stamina among species of animals (e.g., cats *versus* dogs) and among Olympic athletes (e.g., the best sprinters are not the best marathoners). These trade-offs in locomotor performance are based on variation in muscle fiber-type composition and other morphological and physiological characteristics, and possibly variation in motivation.

Are trade-offs ubiquitous? In some cases, expected trade-offs based on mathematical models or on basic biological principles are not found. This may occur because nature has more 'degrees of freedom' than assumed by simple conceptualizations that predict trade-offs. For one example, aside from changes in fiber-type composition, muscles can evolve to be larger, positions of origins and insertions can shift, legs can become longer, and gaits can evolve (including bipedality). As another example, animals may be able to acquire and process more food (e.g., by altering their preferred prey type), thus allowing them to secure more energy and increase both number and size of offspring. Another reason trade-offs may not occur is that 'grade shifts' can change the average values for multiple traits, or even the relationship between traits,

hence causing differences in trait relationships at various phylogenetic levels (Figure 1). Grade shifts may also involve resetting of the basic 'rules' for trade-offs and constraints within a given lineage. For example, snakes, which evolved from lizards, have a different body plan than a typical quadrupedal lizard, which is likely to affect potential trade-offs between speed and stamina. Birds and bats obviously are governed by a very different set of locomotor rules than their non-flying ancestors, and the same goes for whales compared to their terrestrial ancestors. In many cases, the resetting of the rules may have involved the evolution of a key innovation, such as wings or loss of legs. Among species of extant lizards, speed and stamina are only weakly related, but within certain lineages (such as lacertids) speed and stamina show a negative relationship that may be based, in part, on variation in muscle fiber-type composition.

Are trade-offs always between two traits? Although it is easiest to conceive of and recognize trade-offs between only two traits, organisms comprise an almost infinite number of 'traits', and trade-offs may appear only when we include multiple traits in an analysis. The Y-model can be expanded to include multiple traits at multiple levels of biological organization. Speed and stamina might not trade-off in some group of organisms (perhaps even showing a positive relationship), but a composite measure of locomotor performance abilities might be negatively related to one or more aspects of the life history (e.g., growth rate, age at first reproduction, fecundity). Similarly, a physiological or biomechanical trade-off — even if it affects physical fitness (e.g., locomotor abilities) — does not necessarily indicate any trade-off with Darwinian fitness (lifetime reproductive success). Of course, a small effect on a performance trait (e.g., a 2% reduction in speed associated with a 2% increase in stamina) could, for some organisms under some ecological circumstances, make the difference between eating and being eaten.

Does that mean that trade-offs appear only at the extremes of performance? In middle school, I distinctly remember the variation in
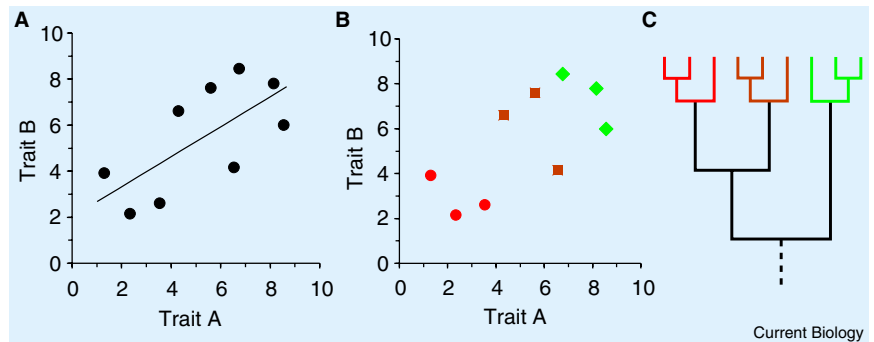

Figure 1. Grade shifts.
Two traits may be positively related among a phylogenetically diverse collection of species (left) (such as vertebrates), but (middle) negatively related when comparisons are made within sets of more closely related species (right) (subclades, such as salmonid fishes or passerine birds).

physical education classes between kids who were generally athletic and those who were not. (Full disclosure: I was somewhere in the middle of the spectrum.) Thus, no trade-off in athletic abilities was apparent. However, when we move from a sample of the general population to the world of elite athletes, we are dealing with a highly selected subpopulation. If you imagine a population composed of the top one percent of sprinters in the original population, the top one percent of marathoners, and the one top percent of decathletes, then a trade-off between speed and stamina emerges — even if they were positively correlated (i.e., the opposite of an apparent trade-off) in the original population.

Are trade-offs inevitable? A negative relationship alone does not prove that two traits necessarily trade-off in a functional or evolutionary sense. Rather, it is possible that natural selection simply never favored the evolution of species that have high (or low) values for both traits. Whether a trade-off (or evolutionary constraint) necessarily occurs can be tested by selection experiments and experimental evolution with tractable model organisms, by phenotypic engineering (such as hormone manipulations), by direct molecular-genetic manipulations, by a search for organisms that break the rules, or by developing a thorough understanding of how organisms work. Finally, it is worth noting that many sexually selected traits, such as the exaggerated tail feathers of male peacocks, may benefit the ability to

obtain mates but hinder escape from predators, reduce foraging ability or increase the energetic cost of locomotion. These situations can also be viewed as trade-offs.

How are trade-offs related to constraints? Constraints can be defined as anything, internal or external to an organism, that limits the production of new phenotypes. For example, if the circulating levels of a hormone change, then any cell that has receptors for that hormone is likely to be affected. Thus, selection favoring increased aggressive or agonistic behavior may have adverse consequences for parental behavior. This example should make clear that, in biology, the concepts of trade-offs and constraints are often closely related.

Where can I find out more?
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