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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,