Design by numbers

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Optimization theory is a branch of mathematics that was developed largely by economists, and which is used enthusiastically by some biologists and viewed with grave suspicion by others. It seeks the best possible solutions to problems: for example, the best investment strategy for a banker, the best breeding strategy for a bird and the best design for a girder or bone.

The structure and behaviour of organisms are moulded by two powerful optimizing processes: evolution and learning by trial and error. Evolution tends to maximize fitness; that is, roughly speaking, an organism's potential for passing its genes on to future generations. Animals may learn, for example, where to go and what to do to maximize food intake, and how to behave to maximize mating opportunity. The incentive to use optimization theory is not to prove that evolution or learning works, but to check our understanding. If my calculations tell me that a particular pattern of behaviour is the best one possible in given circumstances, and if real animals do something quite different, then that suggests that I may have failed to understand the issues in hand.

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Jump to it: theoretical modelling shows that athletes' jumping styles produce optimal results.

In applying optimization theory, we need to be very clear about what 'best', 'circumstances' and 'issues in hand' mean. A typical problem in optimization would have the following form: choose values for variables $x1$, $x2$, and so on, so as to make some function of $x1$ and $x2$ as large (or small) as possible. For example, in an analysis of human high and long jumping, I formulated a simple computer model that predicts the heights and lengths of jumps; I then varied run-up speed ($x1$) and the angle at which the take-off leg is set down ($x2$) and found the combination of $x1$ and $x2$ that gave the highest or the longest jump.

Often in optimization problems, there are limits to the ranges of values that variables can take. In the case of the jumping problem, there is a limit to the speed at which athletes can run. The model led to the conclusion that long jumpers should run up as fast as possible and set down the take-off leg at a steep angle, and that high jumpers should run up much more slowly and set down the leg at a shallower angle. The predicted speeds and angles agreed well with the speeds and angles that successful athletes actually use. The point of the exercise was not to discover the best way of jumping (it seems best to leave that to the athletes and their coaches), but to check that our understanding of muscle physiology is capable of explaining what athletes actually do.

The suspicious attitude of many biologists to optimization theory is exemplified by one of the anonymous reviewers of my proposal for a book that I am currently writing. He or she complained that my outline emphasized optimization of design, "whereas evolution by natural selection often yields suboptimal but adequate design". A comparison of squid and fish might be used to support this view. Squid swim more slowly than typical fish of similar size, but use more energy in the process. The point that has to be understood here is that evolution is constrained by ancestry. A squid is clearly not the best possible swimmer, but it may be close to the best that can be evolved from a mollusc ancestor. An evolving population may be compared to a walker in a mountain range who always walks uphill. Depending on the starting point, this may take the climber to the highest summit, or merely to the top of a foothill. In mathematical language, the squid has failed to reach the global optimum, but it may well be near to a local optimum.

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The anonymous reviewer continued: "Optimization criteria may often be multifold in character and variable in time, rendering a unitary optimal solution an unlikely outcome." There are two good points here. First, natural selection on squid does not work on swimming performance alone, but on the whole suite of characters that influence fitness, and a change that improves swimming may have a detrimental effect on some other function. Second, environmental changes may move the goalposts. However, trade-offs between benefits and harmful side-effects can be taken into account, and in many cases there seems to be little likelihood of the situation being confused by environmental change. (The requirements for swimming will remain much the same until the sea dries up.) The reviewer concluded, grudgingly, that "this is not to suggest that optimal design does not apply in some cases".

Many biologists' concerns about optimization theory seem to stem from a classic paper by Stephen Jay Gould and Richard Lewontin. These authors pointed out that, because evolution is constrained by ancestry, only local optima may be accessible, as in my example of the squid. They also attacked the uncritical use of an inverse optimization approach (if this animal is the answer, what was the question?). The value to biology of properly applied optimization theory has been splendidly demonstrated by Geoffrey Parker and John Maynard Smith, but their message may have to be repeated many times before the doubters are convinced. ■

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Optimization

The structure and behaviour of organisms are moulded by two powerful optimizing processes: evolution and learning by trial and error.

FURTHER READING

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