

The best solution

Optimization: this beguilingly simple idea allows biologists not only to understand current adaptations, but also to predict new designs that may yet evolve.

William J. Sutherland

"If one way be better than another, that you may be sure is nature's way." Aristotle clearly stated the basic premise of optimization in biology, yet it was almost 2,000 years before the power of this idea was appreciated. The essence of optimization is to calculate the most efficient solution to a given problem, and then to test the prediction. The concept has already revolutionized some aspects of biology, but it has the potential for much wider application.

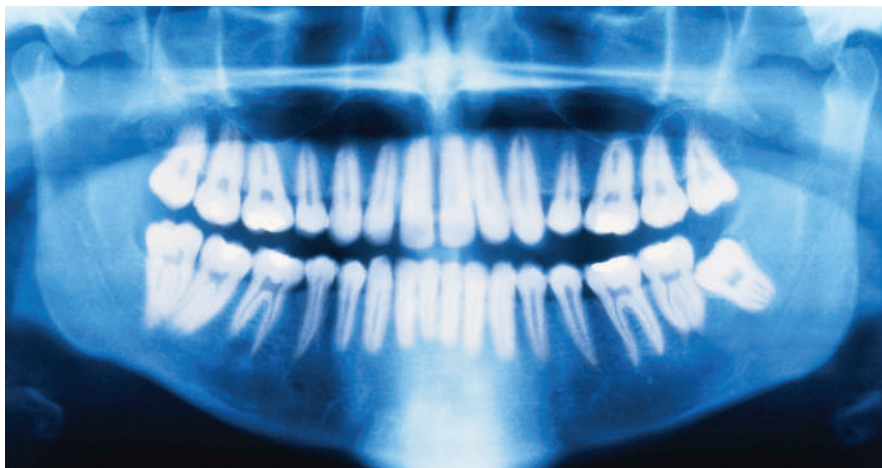
Of course, optimization has long been employed effectively in subjects other than biology. Economists have traditionally calculated the options that result in the greatest profit, and engineers routinely calculate the best design solution, such as the strongest bridge of a given weight.

Darwin's theory of natural selection provided an obvious mechanism for explaining optimization in biology: more efficiently designed individuals will leave more offspring. But it was another century before biologists calculated optimal solutions. David Lack pioneered its use in biology with his concept of the optimal clutch size — the number of eggs that would produce the greatest number of offspring.

The use of optimization has allowed biologists to move from merely describing patterns or mechanisms to being able to predict, from first principles, how organisms should be designed. Optimality models are based on three elements: the choices available; what is being optimized; and the constraints.

Physiologists have used optimization to answer a wide range of questions about animal morphology. For example, optimization has been invoked to predict the design of a bone of given weight that minimizes the risk of breaking or buckling; the speed at which it is most efficient to switch from running to walking; and the gut design that provides the highest energy gain from a given diet. The prediction of the triplet code as the most parsimonious means of coding 20 amino acids using the four bases of DNA is another successful example of this methodology.

But optimization has its critics. The most common objection centres on the mistaken belief that the aim of this method is to test whether organisms are



Revealed: optimal-design theory can be used to assess how selective forces have shaped teeth.

optimal. Actually, it is the assumptions of optimality that are tested. The failure to find support for a prediction can be used to determine whether an assumption is wrong. For example, if animals do not select the diet that maximizes energy intake, it may be because they are choosing a diet that optimizes a balance of different components, or that avoids the costs associated with obtaining larger prey. Once such possibilities have been identified, a new theory can be devised and its predictions tested. It has been argued that this process is circular but in practice it is no different from the successive predicting and testing that underlies most science.

A recent example of the insight that optimization can provide concerns the design of mammalian mouths. It is possible to predict, on the basis of efficient food fracture, how various components of the mouth, such as tooth size, should vary with body size. These predictions can then be compared with actual allometric relationships. Intriguingly, the correlation can be applied to hominid evolution: the traditional approach of predicting morphology from given constraints is reversed to consider how the constraints are likely to have resulted in the observed morphological changes.

Human mouths have become greatly reduced over the past 300,000 years, presumably as we have learnt to fragment food with tools and reduce its toughness with cooking. The predictions from optimal-design calculations are that, for a given body weight, face and incisor size should be directly proportional to the extent to which food is fragmented by

tools. Further calculations give the prediction that the reduction in molars and premolars depends on the cube root of the drop in food toughness. On the basis of these predictions, the changes caused by cooking would have to be vast to match the changes caused by tool use. As predicted, although all teeth have become reduced, the face and incisors have become proportionately smaller. This means the mouth can no longer accommodate the molars, hence the squeezed or missing third molars (wisdom teeth) of many modern humans.

A considerable strength of using optimization is that once we understand why organisms are as they are, then it should be possible to understand how they will respond to new conditions. Optimization can therefore be used to understand behaviour, and to predict population dynamics, in new environments, such as those resulting from habitat loss or a rise in sea level.

There are increasing calls for biology to be predictive. Optimization is the only approach biology has for making predictions from first principles. The wider adoption of these ideas right across biology should reap ample rewards.

William J. Sutherland is at the Centre for Ecology, Evolution and Conservation, School of Biological Sciences, the University of East Anglia, Norwich NR4 7TJ, UK.

FURTHER READING

Alexander, R. M. *Optima for Animals* (Princeton Univ. Press, Princeton, 1996).
Lucas, P. W. *Dental Functional Morphology* (Cambridge Univ. Press, Cambridge, 2004).
Sutherland, W. J. *From Individual Behaviour to Population Ecology* (Oxford Univ. Press, Oxford, 1996).

STONE/GETTY IMAGES

CONCEPTS