3.2 Conceptual and methodological issues in testing the predictions of symmorphosis

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This part of the chapter has three general purposes. First, I present some cautions about optimality models in general and about symmorphosis in particular. Second, I present the quantitative genetic perspective on correlated evolution of different aspects of the phenotype. Third, I consider how one might rigorously test symmorphosis as an evolutionary hypothesis.

Reasons why organisms are not optimal

For various reasons, optimality models are controversial in evolutionary biology. First, organisms are not "designed," and natural selection is not engineering. Although engineers have final goals and purposes, natural selection does not. As well, engineers often design things for a single purpose, whereas organisms must do many things, not just one. In general, nature does not have the luxury of "designing" task-specific organisms. Consequently, "constraints" or "trade-offs" are pervasive in biological systems, and any sort of general or global optimality is exceedingly unlikely to occur.

Second, biological materials have limitations. Although engineers can start from scratch, natural selection cannot. Rather, selection is constrained to work with pre-existing materials (whatever a species happened to inherit from its ancestors), and these might not be the best possible materials for a particular function. For example, whales retain lungs (they have not re-evolved gills) and titanium does not occur in tortoise shells.

Third, energetic efficiency is not necessarily what selection maximizes. Often simply for convenience, optimality models are phrased in terms of energy as the common currency, and the "goal" of selection is seen as maximizing net energy gain or perhaps maximizing energetic efficiency. We have little empirical evidence, however, that this is what selection actually tends to do. Instead, selection generally leads to adequacy or sufficiency, not necessarily optimality.

Fourth, environments are always changing, and selection often cannot keep pace. Selection cannot change organisms extremely rapidly for two reasons: (1) the heritability of phenotypic variation on which selection acts is usually far less than unity, especially for physiological traits; (2) if selection is too strong, then population size will be reduced such that extinction by demographic stochasticity is likely.

Fifth, even if selection could follow the pace of "typical" environmental change, it could not possibly anticipate the effects of major environmental changes, such as asteroids hitting the earth, severe droughts, "100-year floods," or even the invasion of a population by some new pathogenic organism, such as AIDS in the human population.

Sixth, genetic drift operates in all populations and can be strong enough to thwart selection. Thus, genetic drift alone should ensure that average values for populations or species are rarely if ever at the optimum dictated by selection. Indeed, genetic drift is a key element of Sewall Wright's shifting balance theory of evolution, in which it is argued that drift can often push populations in the direction of lower mean fitness.

Seventh, behavior may evolve more rapidly than physiology or morphology, leading to mismatches between what animals do and what they are best suited to do. The dipper (*Cinclus* species) is often cited as an example: it dives and forages underwater, yet is not much different from an ordinary passerine bird in terms of its morphology.

Eighth, sexual selection is largely independent of, and can act counter to, natural selection. Sexual selection, either by male–male competition for access to females or by female choice of particular males, can cause the evolution of bizarre structures and behaviors, such as the tails of peacocks, which are maladaptive with respect to natural selection.

Optimality models can be useful tools

Even if organisms generally are not optimal, optimality models can be useful tools for understanding the evolution of physiological systems. They can indicate the best that organisms could be, given some explicit assumption of a design criterion and within specified constraints. This can facilitate quantitative tests of the degree of departure from perfect design and hence further understanding of the constraints important for

the specific system being studied. Symmorphosis is an informal optimality model, so it can be a useful tool for understanding organismal "design."

Symmorphosis is based on "common sense"

Symmorphosis is based on the notion that animals are built "reasonably," without unnecessary excess capacity – except possibly for appropriate "safety factors." Symmorphosis follows from the idea that maintenance of excess structure is equivalent to wastage of energy and/or space, and hence natural selection should tend to eliminate superfluous structures. This is a very old idea, recognized by Charles Darwin, and invoked by Bennett and Ruben (1979) in their paper discussing the evolution of endothermy: "It is reasonable to assume, however, that these coevolved transport and utilization systems will not differ greatly from each other within an individual animal in their capacity for oxygen processing." They were referring to maximal capacities for oxygen transport, delivery, and utilization, the same physiological system that motivated Taylor and Weibel's original formulation of symmorphosis.

Constraints, trade-offs, and the quantitative genetic perspective on correlated evolution

One reason why symmorphosis might not often occur is that particular structures, and indeed entire organ systems, often must serve multiple functions. For instance, as noted by Lindstedt and Jones (1987), the skin is a (semipermeable) barrier to the external environment, is often damaged and so must be able to heal rapidly, is involved in thermoregulation, osmoregulation, and sensation, and often helps to camouflage an organism. Can such an organ possibly be "optimal" in any meaningful sense? Similar arguments would apply to the respiratory system, which, in addition to its primary function of oxygen transport and delivery, must also get rid of CO_2 and, in many organisms, be involved in thermoregulation and sometimes sound production.

Interactions of the elements within complex systems are often discussed under the general rubric of "constraints" or "trade-offs." One often-discussed example involves possible trade-offs between locomotor speed and endurance: for a given mass of muscle, increasing speed of contraction may come at the price of decreased fatigue resistance.

The framework of quantitative genetics provides one way to think about these kinds of complexities. This branch of genetics was developed for quantitative phenotypic characters that are polygenic (affected by many genes), such as body size or metabolic rate. It provides equations to predict the response to selection, be it natural, sexual or artificial.

For a single character, the equation to predict the evolutionary change of a population's mean phenotype from one generation to the next is very simple: $R = h^2 S$. Thus, if we know what character selection (S) is favoring at the phenotypic level, and the narrow-sense heritability of that trait (h^2, which ranges from 0 to 1), then we can directly predict both the direction and rate of evolutionary change in the phenotype (R).

Organisms comprise far more than just one character. The multivariate version of the above equation is far more complicated: $\Delta \bar{Z} = GP^{-1}S$, where $\bar{Z}$ is the vector of phenotypic means for a series of traits, G is the additive genetic variance–covariance matrix (reflecting narrow-sense heritabilities and genetic correlations), P is the phenotypic variance–covariance matrix, and S is a vector indicating the apparent selection acting on each trait.

Consequently, for multiple traits, the direction and rate of response to selection cannot be accurately predicted in the absence of fairly complete information regarding the selection affecting, and the genetics of, all traits that are correlated with the trait of primary interest. Moreover, many empirical examples indicate that responses to artificial selection are often unpredictable, especially with regard to traits other than the one(s) of primary interest. Accordingly, prediction of the pathway of phenotypic evolution is not easy, and real organisms often may fail to match our "common-sense" expectations.

A graphical model of symmorphosis

Taylor and Weibel argued specifically that when a physiological system is working at its maximum capacity, all steps within the system should be at their maximum, such that none is in excess and so none is, by itself, limiting to overall flux. A simple diagrammatic model of this idea is presented in Figure 3.1. Symmorphosis claims that selection should eliminate "excessive construction," resulting eventually in organisms that correspond to the case on the right of Figure 3.1, in which the capacity of each step is perfectly matched. This state can also be called highly "integrated." An organism fitting the pattern depicted on the right of
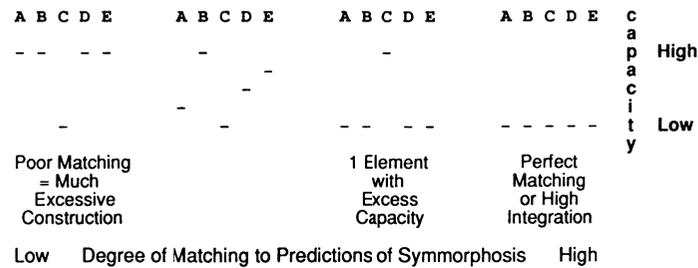
Figure 3.1. A diagrammatic model of symmorphosis, illustrating four possible cases of the matching of capacities of elements (A–E) in a physiological chain. In all four, the maximal capacity of the physiological system (for example, oxygen transport, delivery, and utilization) is the same. In the rightmost case, maximal flux through the system is limited simultaneously by all elements (or, equivalently, it is limited by none). In the leftmost case, flux through the system is limited only by element C, which has the lowest maximal capacity; all of the other elements exhibit "excessive construction". Organisms resembling the case on the left would have "wasteful" excess capacities and hence, symmorphosis predicts, they should rarely exist in nature. Similar to the third case from the left, the mammalian respiratory system often seems to exhibit excess lung capacity, with capacities of other elements fairly closely matched.

Figure 3.1 would be completely symmorphotic, or optimal in some sense. (Note that symmorphosis does not specify how high the maximal capacity of a physiological system should be; only that whatever that maximal capacity (as dictated by selection), all components should be just sufficient in their capacities.) An organism fitting any of the left three patterns depicted in Figure 3.1 would be suboptimal in the sense specified by symmorphosis.

Given such a model of symmorphosis, it should be possible to devise a system to assign a quantitative score for each species or individual animal that one might measure, indicating the extent of wastefulness summed across all of the excessive elements. Supporters of symmorphosis as a generally useful description of animals in nature would expect to find the frequency distribution depicted in Figure 3.2 (top left), with most animals being perfectly symmorphotic (all elements matched in their maximal capacity) or nearly so. The opposite possibility is that most organisms are far from optimal (Figure 3.2, bottom left). If, on the other hand, most organisms are "adequate" or "sufficient," then the frequency distribution of organisms in nature might look something like what is shown in the top right of Figure 3.2. Another empirical possibility is that nature has produced a broad array of organismal diver-
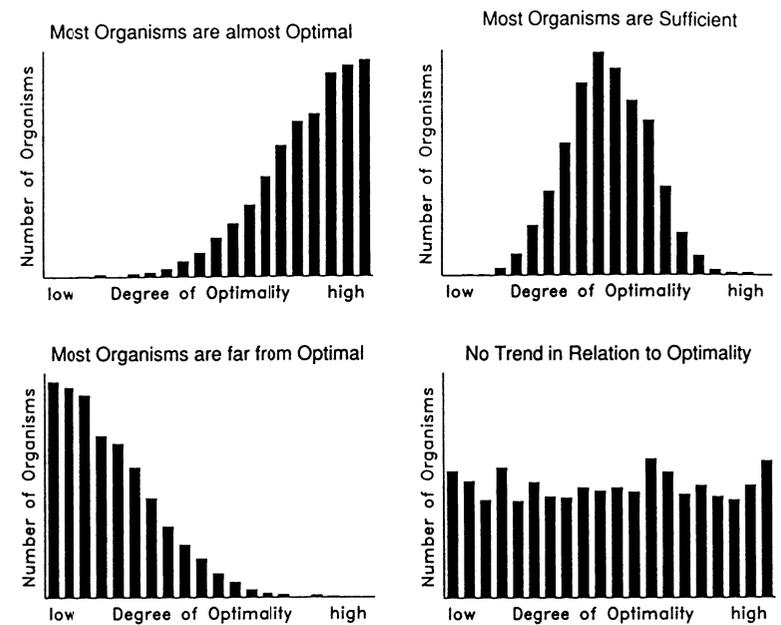
Figure 3.2. Four possible alternatives for the frequency distribution of organisms in nature. The horizontal axis represents the degree of approach to the condition of symmorphosis (defined as close matching of the capacities of components within a physiological system, as depicted on the right of Figure 3.1). Symmorphosis predicts that most organisms are at least nearly symmorphotic (top left), whereas most evolutionary biologists would probably predict that either the top right or perhaps the bottom right is closer to the truth. We currently lack sufficient data to compile such a figure for real organisms, but the significance of symmorphosis as an evolutionary principle will depend on the relative frequency with which its predictions are matched by real organisms.

sity, with some organisms being optimal, others rather poorly "designed," and all possibilities in between (Figure 3.2, bottom right).

Whether most organisms are only crudely integrated, sufficient (adequate), or nearly optimal (perfect) is an empirical question. Tests of symmorphosis by Weibel, Taylor, and their colleagues, with a variety of mammalian species, have produced results that do not indicate perfect matching (rightmost case in Figure 3.1). Specifically, the lung often seems to have excess capacity. As of yet, however, we lack sufficient data to determine the generality of such results for any physiological system in any group of organisms.

A cautionary note about "safety factors"

Most biologists agree that organisms often possess capacities somewhat in excess of what they typically use. Animals, for example, walk most of the time, but they have bodies that can (usually) take the forces experienced during sprint running. From this observation, biologists infer that events which occur only rarely during the lifetimes of individual organisms can nonetheless constitute important selective factors.

Because the concept of safety factors is essentially derived from engineering, whereas organisms are not "engineered," we should be careful about this metaphor or analogy. We should also be very careful in calling *any* excess capacity a safety factor – with the implication that the safety factor is probably optimal in some sense – or else we may fall into the trap of "foregone confirmations", as suggested by Lindstedt and Jones (1987). For example, Karas *et al.* (1987) suggest that "The excess diffusing capacity can be thought of as a 'safety factor' allowing animals to tolerate a decrease in PAO_2 or DLO_2 that may occur normally at altitude or during disease, but it is not clear why this factor should be smaller in the more athletic species." This kind of argument comes perilously close to representing a "just so story" of the kind rightly criticized by Gould and Lewontin (1979). For instance, most organisms (unlike some expeditionary physiologists!) live their lives within a limited altitudinal range, such that symmorphosis would seem to actually predict an elimination of unnecessary "safety factors."

We must be very cautious in accepting claims that every instance of apparent excess capacity represents a "safety factor" (with the implication that it is maintained by natural selection, even though we may admit ignorance as to exactly why) or else we risk tautology and failure to better understand nature. In fact, in no case has a putative "safety factor" in vertebrate physiology or morphology been empirically demonstrated to exist for the implied purpose.

Further reading

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