On Fitness and Adaptedness and Their Role in Evolutionary Explanation

RICHARD E. MICHOD

Department of Ecology and Evolutionary Biology
University of Arizona
Tucson, Arizona 85721

This paper deals with the structure of evolutionary explanations that are based on natural selection. Scientific explanations have two components: the explanandum, or phenomenon to be explained, and the explanans, or that which does the explaining.¹ In evolutionary explanations derived from natural selection, the explanandum is the presence of some trait in a certain frequency or its rate of increase in frequency over time; in other words, the explanandum is usually fitness in the operational sense of Fisher. The explanans of natural selection explanations invariably make reference to design characteristics of the trait, or its adaptedness. Indeed, many evolutionary explanations, such as those that are commonplace in evolutionary ecology, make reference only to adaptedness.

In this essay I discuss situations in which fitness and adaptedness are only indirectly related and are sometimes totally decoupled, in the sense that factors other than adaptedness dominate in the determination of fitness. I argue that one of the main processes contributing to this masking of adaptedness is sexual reproduction. Thus a portion of my argument is concerned with the evolution of sexual reproduction. In my discussion of fitness and adaptedness I distinguish between the intrinsic or genetic aspects of a fitness component and its extrinsic or environmental aspects, and argue that the concept of adaptedness should apply only to the former.

I use the term “fitness” to mean “per capita rate of increase,” a usage that was originally Fisher’s.² Thus the fitness of any type —


2. R. A. Fisher, The Genetical Theory of Natural Selection (Oxford: Oxford University Press, 1930). There are many other uses of the term “fitness” in evolutionary biology. Here I will mention only two of them. “Darwinian fitness” is
for example, of a phenotype, genotype, or trait — is simply its rate of increase divided by the number of the type already present. Fitness, in Fisher’s sense, is defined operationally as a measure of actual evolutionary success. In contrast, adaptedness is a dispositional property or propensity to carry out a specified activity. The “activity” of general interest is survival and reproduction, and I refer here to the propensity to survive and reproduce as “general adaptedness.” Workers more often consider adaptedness for specific activities that are components of general adaptedness (foraging, mating, or predator avoidance, to name only a few). Fitness and adaptedness are central concepts in Darwin’s theory of evolution, as I shall discuss in more detail shortly. Fitness is the bottom line in evolutionary considerations, because it tells whether evolution over a unit of time yields more or less of a type on a per capita basis. An operationally defined quantity, it is relatively easily measured. To explain fitness, however, one must understand its causal components.

The essence of Darwin’s theory, and the “adaptationist program,” is that fitness depends primarily on adaptedness. In other words, the adaptationist position is that the actual rate of increase of a type depends primarily on its functional, adaptive charac-

usually defined as the expected number of offspring produced by a type. Like “Fisherian fitness,” Darwinian fitness is a realized quantity. Another meaning of “fitness” is “adaptedness.” Examples of this usage are in Darwin’s phrase “survival of the fittest” and in the propensity interpretation of “fitness.”


5. There is some disagreement over whether Darwin was a strict adaptationist, as defined by Gould and Lewontin, because he appealed to the “unity of type” as a factor in shaping evolutionary change (see Gould and Lewontin, “Spandrels”; and R. Dawkins, The Extended Phenotype: The Gene as the Unit of Selection (San Francisco: Freeman, 1982). But this disagreement is not relevant to the issue I wish to address, which is whether once a new, better-adapted type arises, its adaptedness is the main determinant of its fitness. I claim that both Darwin and the adaptationist school felt that it is.