Proximate and Ultimate Causations

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Francis (1990) credits me with being "perhaps most responsible for making [the proximate/ultimate distinction] common parlance." Perhaps it is therefore my job to defend it against his attack, which is evidently motivated by his animosity against sociobiology. Since the proximate/ultimate distinction has been adopted by most sociobiologists Francis seems to think that a refutation of this distinction would contribute to a weakening of sociobiology. Let me point out that the stated partitioning of causes goes back in biology at least one hundred years and has been widely used in the ecological and behavioral literature for at least fifty years prior to the coining of the word sociobiology by Wilson.

Francis claims (p. 405) that the distinction proximate-ultimate is superfluous because "we have a perfectly good pair of terms for pairing causes in this way...: 'ontogenetic' and 'phylogenetic'." This claim shows how little he understands these terminologies. All physiological activities are proximately caused, but is a reflex an ontogenetic phenomenon?, or the excretion of urea in the kidney?, or almost any other proximately caused activity?

Francis's attitude is also characterized by the fact that he considers any belief in a genetic contribution to a component of the phenotype as "genetic determinism." It continues to puzzle me why so many authors seem to have so much trouble in understanding that most components of the phenotype are affected both by inheritance and the environment, when it is well known that the 'reaction norm' of the genotype is sometimes very broad.

I feel that it is necessary to correct Francis's misunderstandings of the basic aspects of the proximate/ultimate distinction. Francis's strong anti-genetic bias is also evident from his reference to the "unhappy" genetic program "metaphor" (p. 413). This is now such a standard evolutionary concept, so heuristic in its applications, that it is unlikely that objections by someone close to the behaviorist cause will result in its abandonment.

In order to get clarity, Francis goes to the dictionary for the definition of the word ultimate. It has always seemed to me a dubious procedure to search in a dictionary for authoritative information on a scientific term. Dictionaries almost invariably lag by 20–50 years behind scientific usage. And one must remember that scientific terminologies are usually taken from the daily language and are very often burdened by this heritage. The term selection is a frequently and rightly cited illustration of this burden. This is equally true for the term

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"ultimate," a term that seems to go all the way back to natural theology, and originally meant "caused by God" or "established at the time of Creation." When Baker and Lack reintroduced this terminology, they meant simply "evolutionary causation." In order to shed the historical impediment of the term ultimate, I have used in most of my recent papers the term 'evolutionary' instead of ultimate causation. Also in order not to have a vacuous dictionary definition of ultimate, I specified that ultimate causation means a causation responsible for the shaping of the genetic program. If Francis had paid attention to this specific definition, he would not have needed to fight and refute all sorts of irrelevant meanings of "ultimate."

Francis states correctly that "words are frequently coopted by science and supplied new technical content." But he continues incorrectly, "That is not the case here. No new technical meaning has been supplied to 'ultimate'." In fact such a new technical meaning was supplied by me, by saying that proximate causations relate to "all aspects of the decoding of the information contained in the DNA program of the fertilized zygote" (1976, p. 361) [often with the help of somatic programs, Mayr 1992, p. 129] while the study of ultimate causations concerns "the laws that control the changes of these programs from generation to generation" (1976, p. 361), in other words which cause changes in the DNA of genotypes. These were well defined references to technical definitions of proximate and ultimate (evolutionary). It reveals considerable confusion when Francis finally comes to the conclusion "Ultimate explanations are functional explanations." Incidentally, this is another illustration of the equivocal use of the word "functional" (see Mayr 1992, p. 124). The use of the same word function for physiological processes and for ecological (adapted) roles is inevitably confusing. Francis seems to have intuited this (pp. 411–412) but he failed to draw the necessary conclusions which were correctly arrived at by Bock and von Wahlert (1969). To add another aside: Bringing in the concepts of entropy and equilibrium principle does not add one wit to the understanding of the proximate-ultimate distinction.

I conclude that Francis's comments have not weakened in any way the useful distinction between proximate and ultimate (evolutionary) causations, so widely adopted in the evolutionary literature.

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