

A Broad View of Evolution: A Symposium in Honor of George Williams

A healthy group of prominent evolutionary biologists gathered at Stony Brook University on April 24 at a symposium in honor of George C. Williams, Professor Emeritus in the Department of Ecology and Evolution (Fig. 1). Throughout his long career, Williams has been unique in the breadth of his contributions to the understanding of natural selection and the evolution of behavior. He is one of the few scientists whose insights, without exception, have been fundamentally relevant to all biologists.

Having trained initially in marine biology and earning his Ph.D. from UCLA in 1955, Williams is one of the most prominent living students of evolution by natural selection. His major scientific contribution, *Adaptation and Natural Selection* (1966), corrected the notion, widely circulating at the time, that most or all of an individual's behaviors could be explained as "for the good of the species." This book and subsequent work convincingly brought natural selection back to the level of the individual. Other fields in which Williams has made seminal contributions include the origin and maintenance of sexual reproduction, parental care, disease and senescence, and "Darwinian medicine." In 1999, Williams was a co-recipient, with Ernst Mayr and John Maynard-Smith, of the Crafoord Prize of the Swedish Academy of Natural Sciences, awarded for lifetime contributions to evolutionary theory.

Speakers at the symposium included past students and colleagues of Dr. Williams, and covered most of his major areas of expertise. Two talks specifically tackled the evolution and maintenance of parental care. Mart Gross of the University of Toronto presented models of the trade-off be-



Figure 1. George Williams and his wife Doris at the symposium held in his honor.

tween present investment in offspring (reproductive effort) and investment in one's self (somatic effort), which aids in future reproduction. He showed that many fish species studied in experimental systems, most notably bluegill sunfish, appear to modulate the energy they invest in offspring in ways predicted by the model when faced with different conditions (brood size, past investment, paternity certainty, and future mating opportunities).

George Barlow of the University of California, Berkeley, asked, "How does one decide when a species' pattern of parental care is sex-role reversed?" One of Williams' contribu-

tions to evolutionary theory was a clarification of expected sex differences in parental roles based on purely biological differences (starting with anisogamy) and the specific circumstances in which one would expect these roles to be reversed. Barlow described several cases in which sex roles differed from the paradigm, including some cichlid species in which females are large, highly ornamented, and compete for males.

Randolph Nesse of the University of Michigan Medical School spoke on "Maladaptation and Natural Selection," highlighting Williams' contributions relating to the evolution of disease, senescence, and cases of

apparent sacrifice of individual fitness. Nesse proposed three major answers to the question of why natural selection has left us vulnerable to disease: Natural selection is slow; natural selection is limited—unable to “create” a solution or able to work only in terms of trade-offs; and we misunderstand natural selection. This builds on earlier work by Williams indicating first that the human body is not perfect but constructed within the limits of natural selection, acting proximally on individuals and without foresight, and second, that many conditions assumed to be “pathologies” by non-Darwinian clinicians are often misunderstood adaptive responses or unfortunate results of pleiotropic genes that also code for advantageous traits, probably at earlier life stages.

David Haig of Harvard University provided an update on a related topic, maternal-fetal conflicts during pregnancy. Pre-eclampsia is a well-known condition affecting about 5% of pregnant women in which the endothelial lining of blood vessels is degraded, leading to high blood pressure and other complications. Far from being a simple pathology, as was first assumed, this condition may be an intricate conflict of interest between the developing fetus and the mother, made possible by the intimate blood connection of the anthropoids' hemochorial placenta. The physiological factor thought to induce the condition appears to be secreted by the fetus, which seems to gain from the change. Because the blood supply to fetus and mother is a closed system, increasing maternal blood pressure necessarily increases blood flow and nutrient delivery to the fetus. The gene controlling this “pathology” may therefore be maintained if the benefits to the fetus outweigh the risk posed by reducing the health of the mother.

Another group of speakers undertook the brave task of applying evolutionary principles to behavior in con-

temporary human populations. Bobbi Low of the University of Michigan spoke on “Reductionism and the Complexity of Women's Lives.” She stressed the complexity of female reproduction decisions for modern humans, yet attempted to model them for United States populations, following the assumption that reproductive decisions previously controlled by ecological context would now be controlled by such factors as legal constraints, social and economic status, education, and personal choice.

Finally, Martin Daly and Margo Wilson of McMaster University in Hamilton, Ontario, followed the theme of Mart Gross' earlier discussion of fish choices and considered the trade-off between present and future reproduction in humans. Their detailed analysis of demographic data from seventy-seven long-distinct Chicago neighborhoods showed that homicide rates, largely attributable to young males, were moderately positively correlated with income inequality but strongly negatively correlated with male life expectancy at birth. Specifically, males are more prone to risk-taking behavior when they have more to gain and little to lose, and when future rewards are uncertain due to shorter life spans. They also tested these correlations more directly in a computer-based survey of undergraduates. Test subjects were asked whether they wanted a certain amount of cash immediately or a larger amount after several months. It was quite easy to compute how steeply subjects discounted future rewards relative to present rewards. However, acting on the premise that males and females show different risk-taking behaviors in reproduction, subjects of each sex were shown pictures of “attractive” or “unattractive” members of the opposite sex before the trial was repeated. The group of males shown pictures of attractive females showed significantly steeper

discounting in subsequent trials, indicating that a “procreative” state of mind threw males into a more present-driven mentality. Females' discounting was not affected by the attractiveness of the males they were shown, indicating that females are more level-headed than males, or that, the photographic image most likely to make them lose their cool remains to be discovered.

Primates are ultimately derived from the same stock as sunfish, and have undergone adaptive evolution subject to many of the same rules and constraints. These basic principles are often more easily seen in nonprimates, as they can be teased apart using experimental methods that would either be impractical or unethical if applied to primates. Primatology has many deep roots in ethology and has largely kept up with advances in evolutionary theory. However, it is all too easy to focus on the ways in which primates are different, partly because that is what makes headlines and partly because of a deep-rooted desire in anthropology to understand why and how humans (and, by extension, primates) “rose above the masses.” As the sheer volume of primate research grows, it is both increasingly important and increasingly difficult for primatologists to maintain a broad perspective and keep abreast of continuing refinements in our understanding of how evolution really works. We can only hope that the future will bring us more clear thinkers like George Williams to make this daunting task easier.

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