Steven Frank

Foundations of Social Evolution

Born in 1957. M. Statistics and M.S. in Zoology from the University of Florida in 1983. Ph.D. in Biology from the University of Michigan in 1987. Miller Research Fellow at the University of California, Berkeley, 1987-1989. Faculty member at the University of California, Irvine, 1989 to present, currently Professor of Biology. Interests include host-parasite genetics, symbiosis, and social behavior. — Address: Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697-2525, USA.

I have studied social interactions in biology for many years. I use the word "social" broadly, to mean any interaction in biology in which there is a tension between conflict and cooperation. People most readily identify sociality with the complex behaviors of chimpanzee groups or the remarkable organization of honey bee colonies. I too was drawn to biology because of these popular images.

My own work came to focus on simpler problems. At first glance, the probability that a wasp migrates to another location, or the ratio of sons to daughters produced by a bee, do not seem very much like social phenomena. But biologists have learned that kinship and tensions between individual and group success influence many traits.

Consider, for example, the biology of parasites. Some parasites exploit their hosts in a prudent way, taking the resources that they need without causing noticeable damage. Prudent exploitation yields sustainable benefits to the parasite as long as the host remains healthy. Other parasites attack their host more quickly and vigorously. Rapid exploitation may allow the parasites to achieve higher reproductive rates, but damage to the host reduces the parasites' opportunity for sustainable yield.

I digress briefly to comment on the language of the prior paragraph. To say that "parasites exploit their hosts prudently" seems to impute purposeful or conscious action to a bacterium. What I mean is that bacteria are designed for reproductive efficiency, so sustainable yield is a useful concept in the analysis of bacterial design. But that just shifts the difficulty rather than resolves it, because now I have imputed purpose to the designer. But design without a designer is exactly the problem that Darwin solved. Random bacterial variants arise. Some variants are

reproductively more efficient than others. The efficient variants increase, the inefficient disappear. We only see the relatively efficient, the relatively well designed.

I return now to consider what is "social" about virulence, the amount of damage a parasite causes to a host. Suppose that prudent exploitation of a host maximizes a parasite's reproductive rate. Natural selection then favors each parasite variant, when alone in a host, to follow the prudent strategy. There is, however, a problem when two or more variants occupy the same host. If one variant extracts host resources rapidly and reproduces quickly, then the host may die in a short period. A prudent variant would have relatively low reproductive rate when paired in a host with a rapacious variant because, for both variants, the host is short-lived, and the rapacious variant reproduces more rapidly than the prudent one.

The problem of competing for a shared, limited resource is, colloquially, the "tragedy of the commons". The shared resource may be used most efficiently by slow, prudent exploitation, but rapacious individuals can gain a disproportionate share of the total by rapid exploitation. Each parasite gains most by balancing the benefit from rapid exploitation and the cost of reducing the total resource.

The tension between individual and group success of parasites can be analyzed by biological theories of kin selection. This theory evaluates the contribution of genetic relatedness to the evolution of social characters. Closely related parasites are favored to cooperate and exploit their host prudently, whereas distantly related parasites are favored to compete intensely. Thus multiple infection, with many competing variants and low relatedness, favors rapid exploitation and high virulence.

From traits such as dispersal and virulence, I followed others back to the earliest social puzzle, the biochemistry of life during early evolution. The earliest replicating molecules inevitably competed with their neighbors for essential resources. They also shared a common interest in using local resources efficiently, otherwise more prudent groups would eventually drive overly competitive ones out of existence.

Time and again, when studying problems of virulence or biochemical synergism in early evolution, I found myself confronted with the same conceptual difficulties. The standard ideas, such as biological kinship, were almost the right tool to clarify the logic of a problem. But often I had to invent new methods of analysis. This led me to believe that the standard, core concepts of social evolution were, as I said, almost right, but at bottom there was more work to be done. One could not move easily from the basic ideas, which sounded right, to a clear and complete logical analysis of many problems.

I decided to spend my year at the Wissenschaftskolleg on those conceptual problems that recurred with each new biological puzzle that I had studied. Could I clarify in a significant way the basic concepts, the foundations of the field?

My approach was to write a "how-to" guide for analyzing social problems in biology. My ultimate plan was to cover all the major topics: the original of social groups, the dynamics of conflict and cooperation, and various sexual phenomena. This was, of course, too much for one year. I found, as I wrote, that a full volume should be devoted to the basic conceptual tools of the subject. I completed the volume, and inevitably discovered along the way that I had to solve several new problems to fill in the foundations.

The Wissenschaftskolleg was an ideal place to do this work. It is my only encounter with an institution that provides a perfect atmosphere for scholarship, at once playful and serious. And it is one of the few places in the world at which a scholar is expected to be just a scholar, nothing more and nothing less.