literature. Some hunter-gatherer societies appear to have leaders who possess a higher status than other members of their group. However, these individuals are usually more like elected officials than dominators. Only the most fair-minded are chosen, their ongoing behavior is subject to intense moral scrutiny, their role is to advise rather than dictate, and their authority is often restricted to certain domains. As a result, the potential for natural selection within groups is curtailed.

Groups of hunter-gatherers make myriad decisions on a daily basis and periodically are faced with more momentous decisions in emergency situations. Most of these issues are discussed in public with the goal of reaching a decision that can be executed by the entire group. Shared decisions increase behavioral uniformity within groups and concentrate behavioral differences at the between-group level. For example, groups that are faced with a severe food shortage may need to decide whether to hunt a particularly dangerous type of game. Individuals in each group may disagree about the best decision, but these differences of opinion will not be manifested as behavioral differences if the group reaches and acts upon a decision as a unit. Instead, groups will differ in their behavior, and the members of any given group will be in the same boat with respect to survival and reproduction.

Punishing free-riders in hunter-gatherer societies is complicated by the fact that some individuals deserve a free ride, when they are disabled or otherwise unable to contribute to group efforts. The egalitarian ethic provides a safety net for those in legitimate need, which opens the door to simple laziness. Nevertheless, the same social mechanisms that are effective against would-be dominators can be used against illegitimate free-riders, especially during periods of hardship. Boehm describes one example in which an Inuit Eskimo family with a long history of stingy behavior lived at the periphery of the group and was denied many social benefits.

Boehm believes that human social groups have been guided by an egalitarian ethic for many millennia, long enough to have influenced both genetic and cultural evolution. By controlling behavioral differences within groups and increasing behavioral differences among groups, the egalitarian ethic shifted the balance between levels of selection and made group selection an important force in human evolution. The organismic view of human society may therefore be partially justified, but Boehm stresses that much of human nature remains a product of within-group selection. Multilevel selection theory may explain both our remarkable ability to build adaptive social organizations, and our more disturbing ability to tear them down.

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NOTA BENE: IMMUNOLOGY

Population Biology of Lymphocytes

The aphorism that immunologists "know everything and understand nothing" about their subject has long since passed its sell-by date. Nevertheless, one area of immunology that continues to frustrate is homeostasis—how are lymphocyte numbers, life-span, and population dynamics controlled? What factors influence the interaction of lymphocytes with their environment and with each other?

Substitute the word "lymphocytes" with "organisms" and you have a loose definition of the science of ecology. Building on this similarity, a recent paper in the *Proceedings of the National Academy of Sciences* (*1*) provides a new approach to the study of lymphocyte homeostasis. It uses formal ecological competition theory to design and interpret a series of experiments that test how competition for limiting resources regulates peripheral B cell numbers in adult mice. The candidate-limiting resource is antigen: a B cell expresses only one of an almost infinite number of antibody types on its surface, so the amount of antigen in the environment recognized by any one cell is likely to be limited. If, as seems likely, antigen is necessary for the survival and proliferation of B cells, access to antigen may be relevant to homeostasis.

The work started with a series of predictions generated by applying the Lotka-Volterra competition model to lymphocyte production, competition, and death. (In the 1920s V. Lotka and A. J. Volterra proposed a model of population dynamics that related the reproductive rates of individual organisms to the densities of their own species and of competitor species.) These predictions were then tested experimentally in vivo: The B cell compartment of irradiated mice was repopulated with bone marrow from normal mice or mice expressing an immunoglobulin transgene, and the resulting pool of mature B lymphocytes in the spleen was analyzed.

The normal bone marrow yielded a population of mature B cells that expressed a wide range of surface antibody types, whereas a much more restricted range of antibodies developed when bone marrow from the transgenic mice was used (because the transgene suppresses rearrangement of the germline immunoglobulin genes). The splenic B cell populations generated independently by the two types of bone marrow were the same size. However, when the bone marrow stem cell populations were mixed, B cells derived from the normal bone marrow outnumbered the transgene-expressing population. Was this due to the greater ability of the diverse population to compete for a limiting resource, as predicted by the model? Apparently so, because repetition of the experiment in the presence of the antigen that is recognized by the transgene gave the transgenic B cell population the upper hand. Thus, resource availability (in this case antigen) seems to be crucial for B cell homeostasis, consistent with the long-standing observation that mice never exposed to exogenous antigen have few B cells (*2*).

Many of the important scientific themes in ecology—stability, competition, predator-prey interactions, host-parasite interactions, mutualism, and detrivory—have obvious parallels in immunology. Further borrowing of ecological theory by immunologists is likely, especially if practical applications can be demonstrated. In the current example, practical spin-offs might include the design of multivalent vaccines: Rational decisions about the composition of the vaccine are hindered by interference among the various components. This work develops the appropriate theoretical framework to begin to describe and circumvent these constraints.

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