protein in *Xenopus* oocytes causes the coordinate inhibition of most Ran-dependent import and export pathways, thereby implicating Ran as the target of M protein. The fact that tRNA export, which is independent of the Ran system (9), is not inhibited by M protein is consistent with the hypothesis that the Ran gatekeeping system is the M protein target. If M protein uses a preexisting cellular mechanism to inhibit nuclear transport, then the identification of the factors that interact with M protein may reveal important components of the Ran control apparatus.

Both reports in this issue leave us wondering about the control of the Ran switch in the nucleus and cytoplasm. Perhaps, when the control apparatus is revealed, the VSV M protein will already have its finger on the mechanism.

References

1. S. A. Richards, K. L. Carey, I. G. Macara, *Science* **276**, 1842 (1997).
2. L.-S. Her, E. Lund, J. E. Dahlberg, *ibid.*, p. 1845.
3. D. S. Gorlich and I. W. Mattaj, *ibid.* **271**, 1513 (1996); E. A. Nigg, *Nature* **386**, 779 (1997); J. Moroianu, *Crit. Rev. Eukaryotic Gene Expr.* **7**, 61 (1997).
4. V. W. Pollard *et al.*, *Cell* **86**, 985 (1996); J. D. Aitchison, G. Blobel, M. P. Rout, *Science* **274**, 624 (1996); S. Nakielny *et al.*, *Exp. Cell Res.* **229**, 261 (1996); N. R. Yaseen and G. Blobel, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 4451 (1997); N. Michaud and D. S. Goldfarb, *J. Cell Biol.* **112**, 215 (1991); M. P. Rout, G. Blobel, J. D. Aitchison, *Cell* **89**, 715 (1997).
5. D. Goldfarb and S. Grapes, *Curr. Biol.* **4**, 57 (1994); D. Gorlich *et al.*, *EMBO J.* **15**, 5584 (1996); K. Weis, C. Dingwall, A. I. Lamond, *ibid.*, p. 7120; M. K. Iovine and S. R. Wente, *J. Cell Biol.* **137**, 797 (1997).
6. T. Tachibana *et al.*, *FEBS Lett.* **397**, 177 (1996); A. H. Corbett and P. A. Silver, *J. Biol. Chem.* **271**, 18477 (1996); B. M. Paschal, C. Delphin, L. Gerace, *Proc. Natl. Acad. Sci U.S.A.* **93**, 7679 (1996); P. Percipalle *et al.*, *J. Mol. Biol.* **266**, 722 (1997); W. D. Clarkson, H. M. Kent, M. Stewart, *ibid.* **263**, 517 (1996).
7. R. Mahajan *et al.*, *Cell* **88**, 97 (1997); H. Saitoh, R. Pu, M. Cavenagh, M. Dasso, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 3736 (1997); M. J. Matunis, E. Coutavas, G. Blobel, *J. Cell Biol.* **135**, 1457 (1996).
8. M. Ren *et al.*, *Mol. Cell Biol.* **15**, 2117 (1995); K. M. Lounsbury and I. G. Macara, *J. Biol. Chem.* **272**, 551 (1997); S. A. Richards *et al.*, *J. Cell Biol.* **134**,1157 (1996); A. S. Zolotukhin and B. K. Felber, *J. Biol. Chem.* **272**, 11356 (1997).
9. Y. Cheng, J. E. Dahlberg, E. Lund, *Science* **267**, 1807 (1995).

EVOLUTION

Human Groups as Units of Selection

David Sloan Wilson

Holistic thinkers throughout history have compared human societies to single organisms. Modern scientists have tended to dismiss the organismic view of society as a misleading metaphor, but a recent article by anthropologist C. Boehm, director of the Jane Goodall Research Center at the University of Southern California, suggests that it may contain an element of truth (*1*).

Boehm's article appears in a supplemental issue of *The American Naturalist* devoted to the subject of multilevel selection (*2*). Natural selection within a single population can explain the functional design of individuals, which causes them to survive and reproduce more successfully than their neighbors. However, this process cannot explain the evolution of altruistic behaviors, which are good for the group but, nevertheless, decrease the relative fitness of the altruistic individual within the group. Even behaviors that benefit the group as a collective, at no cost to the individual, are merely neutral from the standpoint of within-group selection. Darwin was aware of this problem and proposed that natural selection can operate at more than one level of the biological hierarchy. Altruists may be less fit than nonaltruists within a single group, but groups of altruists are more fit than groups of nonaltruists. Groups can evolve into adaptive units if the process of group selection is sufficiently strong, relative to the process of individual selection.

One for all... The !Kung tribespeople, a hunter-gatherer society in Africa, foster an egalitarian society by using group decision-making. [Courtesy of Irven DeVore/Anthro-photo]

The organismic view of human society can therefore be scientifically justified, but only if group selection has been a significant force in human evolution. Most evolutionary biologists have dismissed this possibility, because they believe that group selection requires extreme genetic variation among groups. Boehm's article suggests that other factors caused group selection to be important in human evolution, despite the fact that human social groups are genetically diverse.

According to the new work, virtually all hunter-gatherer societies have an egalitarian ethic that makes it difficult for individuals to increase their fitness at the expense of other individuals in the same group. The impulse to dominate and surpass one's neighbors is not absent, but it is successfully resisted by pressure from other members of the group in most cases, resulting in what Boehm calls a reverse dominance hierarchy. The egalitarian ethic causes meat and other important resources to be shared among the entire group, circumscribes the power of leaders, punishes free-riders, and causes virtually all important decisions to be made by a consensus process. As a result, the egalitarian ethic accomplishes a degree of behavioral uniformity within groups, and differences between groups, that could never be predicted from their genetic structure.

Boehm focuses on three implications of egalitarianism for multilevel selection theory: thwarting the ambitions of would-be dominators, making decisions as a group, and punishing free-riders. The egalitarian ethic includes a set of social norms that define the dos and don'ts of the society. Striving to achieve at the expense of other members of the group ranks high among the don'ts, and few individuals are powerful enough to resist the collective moral outrage of their neighbors. Mild forms of social control, such as gossip and withholding social benefits, are usually sufficient to control would-be dominators, but more extreme measures, such as ostracism and execution, are recorded in the ethnographic

The author is in the Department of Biological Sciences, Binghamton University, Binghamton, NY 13902–6000, USA. E-mail: dwilson@binghamton.edu

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.

References

1. C. Boehm, *Am. Nat.* **150**, S100 (suppl.) (1997).
2. Special issue on Multilevel Selection, D. S. Wilson, Ed., *ibid.*, **150** (suppl.) (1997).

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.

References

1. A. R. McLean, M. M. Rosado, F. Agenes, R. Vasconellos, A. A. Freitas, *Proc. Natl Acad. Sci. U.S.A.* **94**, 5792 (1997).
2. B. S. Westman, E. Bruckner-Kardos, J. R. Pleasant, *J. Nutr.* **112**, 562 (1982).

—**Richard B. Gallagher**