to Washington or chairing administrative meetings. Although he's vocal on technical issues, he acknowledges that he becomes "shy when jostling for a position." He recalls a meeting of U.S. and European physicists where everyone literally fought for the best seat. "I told my wife that night, 'I don't belong here.' "

Americans of East Asian heritage say that they must constantly navigate the conflicting currents of their two cultures. "I've tried—consciously—to be as Americanized as I can," says Luo, as she bustles around her office. "Until Asian-American scientists can understand the differences and purposefully try to melt into this culture a little bit better, there will be problems." But others put an emphasis on what their native cultures can bring to the lab—such as a more careful and collaborative approach. "Since we come from a basically poor resource environment, we usually plan two or three steps ahead," says Livermore's Joel Wong. And the East Asian tradition of collaborative efforts, as opposed to the rugged individual model of the West, is a good fit for an era of large and complex scientific endeavors, he adds. And, Wong says, "I don't want to lose my cultural traits. Each immigrant brings to this country a gift."

But the hard lesson from the Lee case, says Berkeley's Wang, is that Asian Americans must learn to play by traditional American rules when necessary: "It's fine to retain our traditional cultural values, but democracy only works for those who participate." If you don't take part, he adds, "you'll be run over." But there is an alternative—at least for those who have not been in the United States for generations—Wang notes. An increasing number are voting with their feet by moving to the booming universities and high-tech companies of Hong Kong, Singapore, Taiwan, and South Korea, which often offer tempting salaries, benefits, and working conditions. "The best and brightest will move on, which will hurt American science," worries Henry Tang, chair of a New York–based group of prominent Asian Americans called the Committee of 100. Adds Wong: "So if this country wants to avoid a reverse brain drain, it will have to accommodate us."

–ANDREW LAWLER

EVOLUTIONARY BIOLOGY

In Search of Biological Weirdness

William D. Hamilton was drawn to the unusual and paradoxical. His observations led to new insights into social interactions and sex

BERKELEY, CALIFORNIA—The late William D. Hamilton (1936–2000) liked to dwell on the fringes of biology. When most of his colleagues were caught up verifying natural selection and survival of the fittest, fairly straightforward aspects of evolutionary theory, Hamilton was instead drawn to life's apparent paradoxes. Why, for instance, do individuals make sacrifices for others instead of just looking out for themselves? Or why does sex exist, given that asexual reproduction is a more efficient way to pass on all of one's genes? A dedicated student of nature—some say he was the quintessential eccentric British naturalist—Hamilton had an eye for the unusual: the fig wasp that produces mostly female progeny instead of equal numbers of both sexes, the sterile worker bee who nevertheless works hard for the good of the hive. He thought deeply about how these arrangements might have evolved.

Those thoughts and the theories that resulted have inspired a generation of evolutionary biologists, providing them "with a scientific basis for studying the weirdest possible things," says Wayne Getz, an applied mathematician at the University of California, Berkeley. Getz, Berkeley's Phil Starks, and Robert Page of the University of California, Davis, organized a symposium here in October to honor this giant of evolutionary biology, who died of malaria in March at age 63. There, they and about 70 others discussed where Hamilton's ideas have taken them.

By studying life on biology's fringes, "you can begin to understand how the whole [of life] is constructed," Getz explains. Just as the gaudiness of a peacock's tail helped tip off biologists that a female's choice of mate was important in evolution, extreme lifestyles and living arrangements help researchers discern other hard-to-see biological principles. A few researchers, such as Francis Ratnieks of the University of Sheffield, United Kingdom, have found exquisite support for some of Hamilton's ideas. Others, like Getz, are coming up with theories that complement those Hamilton proposed.

Ever the field biologist. William D. Hamilton, here in Africa, believed that almost all ideas were worth pursuing.

CREDIT: JEFFREY B. JOY

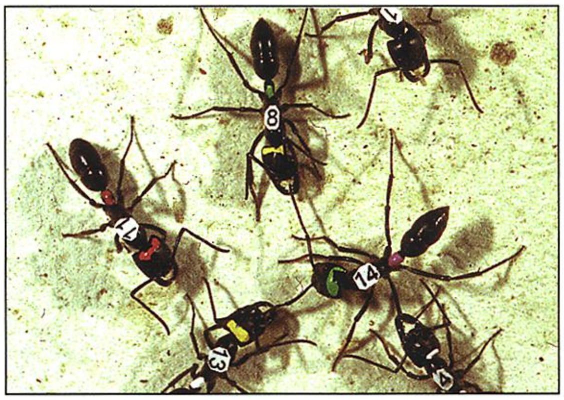
All in the family

Hamilton's work on what he called inclusive fitness is seen as perhaps his most important contribution to biology. In 1963, Hamilton introduced the idea that social groups would evolve if there were enough additional benefits, in terms of passing on an individual's genes, to those participating in the group. That added benefit exists because each individual shares certain genes with relatives—the number depending on how closely related they are. So, to varying degrees, each relative's young helps perpetuate an individual's genetic legacy. Hamilton argued that participation in the group should vary according to the benefit each individual received.

He also realized that because self-interest is always partially at odds with group needs, individuals might vie to tilt the odds in favor of their own genes being passed on—even if that meant cheating on their fellow group members. As a result, conflicts could arise among group members. "The work revolutionized our understanding of reproduction, altruism, cooperation, and conflict," says Ratnieks.

Ratnieks has been exploring the conflicts that arise in social groups of ants. "We have used inclusive fitness theory to make novel predictions about areas of social life that were not [explicitly] covered by the theory before," he explains. In particular, he and Sheffield's Thibaud Monnin have been looking at how hierarchies develop and persist within ant colonies and how worker ants make sure that as many of their genes as possible are passed on even though they themselves are not laying any eggs.

In preliminary research with several large ant species belonging to the genus *Dinoponera*, Ratnieks has found how members of the colony keep other members from gaining a reproductive edge over their nest mates and, in the process, make it less attractive for other ants to even try to gain that edge. In this way, workers maximize the size of their genetic bequest in each egg laid. "[Hamilton's] theory [is] remarkably close to what is observed," says Ratnieks.



Social tension. Worker ants help protect the colony's egg-laying ant by intimidating an upstart (14) that challenges her.

In these colonies, all ants look alike and can reproduce; there is no queen, as there is in a honeybee hive. But the ants nevertheless have adopted a hierarchical structure in which one alpha ant, or "top dog," does almost all the reproducing. After she mates with a male at the start of her reproductive life—which she does just once—she does little else besides lay eggs. The majority of other ants are workers who forage for food, tend the eggs, and maintain the nest. They are at the low end of the pecking order. In between are several high-ranking ants called "hopeful nonworkers": They don't work and try to become egg-layers instead.

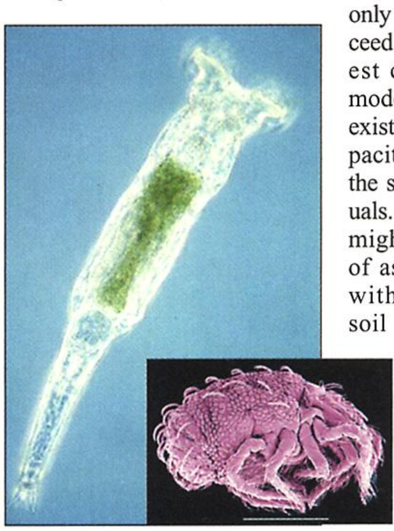
Given the appeal of that easy life, Hamilton's theory would predict that lots of workers would opt to be hopeful nonworkers, taking the chance that they would eventually become the egg-layer—the one who gets to pass on her genes all the time. But only a few do, so Ratnieks and his colleagues decided to figure out why.

One reason, Ratnieks and his colleagues found, is that the life of a hopeful nonworker is a rough one—and that provides one clear disincentive to many ants that would otherwise strive to move up in the hierarchy. Both the alpha ant and many workers try to prevent any upwardly mobile ants from laying eggs. The alpha female often grabs the antenna of her rival, preventing it from bullying lower ranking individuals. Sometimes, she bites a rival's antenna and rubs it against her belly, as if to make clear who is boss. Combining forces, a number of workers will each grab the leg or antenna of an uppity individual, particularly the number-two ant, holding her spread-eagle "sometimes for days," says Ratnieks. By that time, she is sufficiently intimidated and likely will be unable to lay eggs. The worker ants' reaction to hopeful nonworkers fits well with Hamilton's view, as individuals are working to maintain their own self-interest even as they are contributing to group living.

In terms of self-interest, this policing behavior makes sense because most of the workers—including the upstart rivals—are daughters of the egg-laying alpha ant. Hamilton would have predicted that because more of the workers' genes are passed on when their mom reproduces than when their sister does, the workers would prefer to have their mom do all the egg-laying. That's second only to being able to lay the eggs themselves. "It's not in their interest" for workers to allow the alpha female to be replaced, explains Ratnieks. Moreover, each ant that becomes a hopeful nonworker diminishes the colony's productivity; if too many ants make that choice, the colony as a whole suffers. Although these results are preliminary, they are "an extremely clear and elegant application of Hamilton's inclusive fitness theory to explain social interactions and conflicts," comments Stuart West, an evolutionary biologist at the University of Edinburgh, United Kingdom.

The when and why of sex

Sex—specifically, why it is necessary—was another of Hamilton's pet problems. Asexual reproduction seems the most efficient way to pass one's genes to the next generation, as each offspring is essentially a clone carrying 100% of the parent's DNA; in sexual reproduction, by contrast, each parent contributes only half. But sex persists—indeed, it is the dominant form of reproduction among vertebrates and exists in many other kinds of organisms. Geneticists have come up with one explanation for the persistence of sex. In asexual reproduction, they suggest, the clones would accumulate genetic mutations through successive generations that would eventually render the organism dysfunctional. Sexual reproduction could help remove these mutations, as parents with one bad and one good copy of a gene can each pass that good copy on to the offspring, removing the bad copies from the genome.



Sex or no sex? Hamiltonians want to know what makes a mite (*right*) sexual or asexual and why all bdelloid rotifers (*left*) are asexual reproducers.

But Hamilton had a different idea: Only through genetic variety, which sexual reproduction brings, could organisms have any hope of outwitting parasites. In the evolutionary arms race, microbes reproduce and change so quickly that they can rapidly evolve ways to avoid the host's defenses. The new combinations of genes that sex provides give the host a much-needed edge—an advantage that outweighs that of passing on a full set of genes, Hamilton suggested.

Neither of these theories has thoroughly convinced researchers. For one, they don't explain why some organisms have switched back and forth between the two forms of reproduction over evolutionary time, sometimes practicing both. Nor do they explain why others, such as the much-studied group of single-celled aquatic organisms called bdelloid rotifers, don't bother with sex at all.

Now Getz thinks he has an answer to why organisms might be sexual, asexual, or both. He has developed a mathematical model that enables him to predict which type of reproduction will exist within a community. The model assumes that each clone produced by asexual individuals will use the local resources in the same way; sexual reproduction, on the other hand, will provide different gene combinations that enable offspring to exploit the environment in multiple ways.

If the environment never changes, clones could win out, simply because their genes would come to dominate the population. But the model shows that the more the environment fluctuates, the more likely it is that only sexual organisms will succeed. Under conditions of modest change, though, the two modes of reproduction can coexist, with the reproductive capacity of clones balancing out the survival capacity of the sexuals. Getz thinks this hypothesis might explain the coexistence of asexual and sexual species within particular genera of soil mites. As for asexual rotifers, Getz proposes that they have a different way of avoiding extinction when their environment changes. Rotifers can survive droughts, because their eggs desiccate and persist in the soil until rehydrated when the right environment "returns."

CREDITS: (TOP TO BOTTOM) T. MONNIN/LAB OF APICULTURE & SOCIAL INSECTS, SHEFFIELD UNIVERSITY; (MITE) D. WALKER; (ROTIFER) MESELSON *ET AL.*

"[Getz] provides an interesting new perspective," says Lotta Sundström, an evolutionary biologist at the University of Helsinki, Finland. However, she and West both caution that Getz has not captured the full picture. West in particular thinks the best model will be more inclusive and will factor in the value of sexual reproduction in ridding the genome of mutations and also in enabling organisms to deal with parasites.

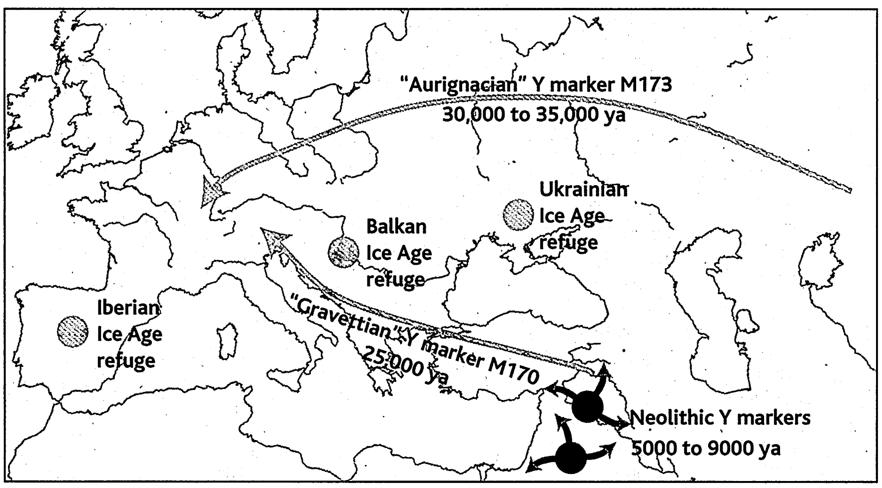
Getz takes their criticism in stride. Like Hamilton, he's open to considering a wide range of possibilities about how life works and gives serious thought even to farfetched ideas. Hamilton's career, he notes, demonstrated how such open-mindedness can have great rewards. "When we begin to think with a Hamiltonian frame of mind," Getz explains, "it allows us to consider astonishing kinds of phenomena"—and sometimes even figure them out. **–ELIZABETH PENNISI**

EVOLUTIONARY GENETICS

Europeans Trace Ancestry To Paleolithic People

Y chromosome data show that living Europeans have deep roots in the region—and researchers say genetic markers may be linked to archaeological cultures

About 8000 years ago, the people living in Franchthi Cave in southern Greece experienced a dramatic change of lifestyle. On the floor of the cave where hunter-gatherers had been dropping stone tools and fishbones for thousands of years, the remains of a new kind of feast appear: traces of wheat, barley, sheep, and goat, which can only be the result of farming and herding animals. Within the next 3000 years, the same abrupt transition ripples through archaeological sites along the shoreline of the Mediterranean, eventually reaching Europe, where settled villages of mud-brick houses appear. "The consequences of the transition were fundamental—village settlement, new beliefs, different social structure," says archaeologist Colin Renfrew of the University of Cambridge in England. "A behavioral revolution took place."



Men on the move. Y chromosome data reveal three major migrations into Europe, which researchers tie to known archaeological cultures. At 40,000 years ago (ya), the Aurignacian people moved in (green), followed by the Gravettians 25,000 years ago (blue), and finally the Neolithic farmers (red) 9000 years ago.

CREDIT: G. PASSARINO AND P. UNDERHILL/STANFORD UNIV.

But which people made that revolutionary European transition? Did farmers move into Europe from the Fertile Crescent in the Middle East, or did local hunter-gatherers learn to trade and farm themselves? And if Neolithic newcomers brought farming technology, did they replace most of the locals, or did those Paleolithic locals survive and become the primary ancestors of modern Europeans?

Now, after years of debate, these questions are being answered not only by ancient remains but also by the genes of living Europeans. In a report on page 1155, an international team reports that a wealth of data from the Y chromosome show that it was the local hunter-gatherers who passed on more of their genes. More than 80% of European men have inherited their Y chromosomes—which are transmitted only from father to son—from Paleolithic ancestors who lived 25,000 to 40,000 years ago. Only 20% of Europeans trace their Y chromosome ancestry to Neolithic farmers. Thus, the genetic template for European men was set as early as 40,000 years ago, then modified—but not recast—by the Neolithic farmers about 10,000 years ago.

These Y chromosome data are "strikingly similar" to new findings on mitochondrial DNA (mtDNA), which is inherited maternally, notes evolutionary geneticist Martin Richards of the University of Huddersfield in England, who led a mtDNA study published in the November issue of the *American Journal of Human Genetics*. "A consensus is emerging on what the genetic data are telling us," says Richards. "After all the debate, this is very exciting and encouraging."

The data from both genetic lineages not only enable researchers to trace the movements of the first farmers, they also paint a remarkably detailed picture of the identity and movements of ancient Europeans. The Y chromosome team, led by geneticists Ornella Semino of the University of Pavia in Italy and Giuseppe Passarino of Stanford University, also took the bold step of explicitly connecting genetic and archaeological data—a move that is already drawing some fire. The researchers link two early migrations recorded by the Y chromosome to two Paleolithic cultures, the Aurignacian and Gravettian, each famous for their spectacular art and artifacts (see map). "This paper shows us that molecular genetics is beginning to show us which genetic markers are coordinated with climatic events and population dispersals," says Renfrew.

The earliest glimpse of European genetic origins came from protein markers; more recently, researchers studied the mtDNA of European women. But the results were divided: One group of researchers that included Stanford geneticist L. Luca Cavalli-Sforza, a co-author of the new Y chromosome study, found similar markers in Europeans and Middle Easterners, which declined from east to west and looked like the signature of the Neolithic expansion. But other researchers proposed that several European genetic markers were too old to have been introduced with the Neolithic newcomers.

The obvious way to reconcile the sometimes heated debate was to look at men's genetic history as recorded on the Y chromosome. By comparing the variations, called polymorphisms or markers, at one site on the chromosome, and the frequency at which those variations occur in different populations, geneticists can sort out which populations are most closely related. They can then build a phylogenetic tree that traces